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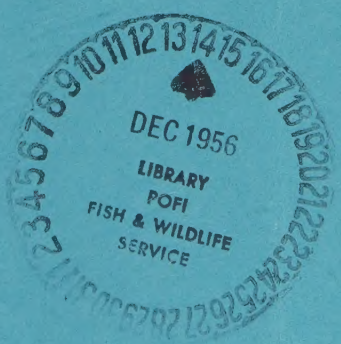


SCOTTISH HOME DEPARTMENT

Marine Research
1956 No. 4

Eggs and Larvae of Haddock (*Gadus aeglefinus* L.) at Faroe

By ALAN SAVILLE, B.Sc.



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CONTENTS

	Page
Introduction	3
The Area	3
Material	4
Separation of Cod and Haddock Eggs	4
Spawning Season	5
Spawning Areas	6
Day and Night Variation in Catches of Larvae	9
Distribution of Larvae in Time and Space	10
Growth	11
Estimation of Annual Egg Production	16
Larval Abundance and Larval Mortality	20
Discussion	24
Summary	25
References	26

Eggs and Larvae of Haddock at Faroe

INTRODUCTION

Brood fluctuations have long been recognised as one of the major factors affecting the magnitude of the fishable stocks of almost all species of commercial fish. Their cause or causes, however, remain a problem for the fisheries biologist as well as for the industry. Variations in the strengths of broods before they enter the commercial stock could be caused by (1) annual variations in egg production or (2) differential mortality during the planktonic and/or the early demersal stages. Heavy mortality during the planktonic phase has been the cause widely favoured by marine biologists, largely on theoretical grounds and following the lead given by Hjort (1926). This belief has, however, been given greater weight by Parrish (1950). He found for the North Sea haddock stock that (*a*) the recruit level of brood density is largely independent of the size of the spawning stock and that (*b*) no large-scale differential mortality occurs from the time young haddock take to the bottom until they enter the commercial stocks. The time seemed ripe for a systematic investigation of the planktonic phase of a haddock stock.

Such an investigation was conceived as having two major aims. The first was to see whether Parrish's findings could be confirmed and strengthend by ascertaining whether (*a*) the recruitment to a commercial stock was independent of its egg production rather than of the size of the stock within the level of fluctuations normally encountered, and whether (*b*) the number of recruits could be related directly to the abundance of a late pelagic stage and not merely to the subsequent early demersal one. The second and more important aim was to obtain a measure of mortality between successive stages of the planktonic phase. If brood fluctuations are due to differential mortality during the planktonic phase there would appear to be two possibilities. Either there could be a shortage of recruits due to a slightly above-average mortality throughout the entire planktonic phase, or the same result could proceed from a very heavy mortality operating during only a short part of the phase. In the latter case the search for the causal environmental factors could be narrowed considerably.

It might have seemed more logical to have tackled this investigation in the North Sea where Parrish's work was done. There were, however, two considerations against this course. Firstly the spawning area of the species within the North Sea is so large that it could not be adequately sampled with the resources available, and secondly the situation in that area is rather complicated by the possibility of the indigenous stock being augmented by planktonic stages carried into the area from spawning centres off the Scottish north and west coasts. Accordingly it was decided to tackle the problem at Faroe where the stock is thought to be self-contained and its area of distribution is circumscribed and fairly small.

In each of the years 1950-53 the Faroe area was sampled during the time when planktonic haddock stages were to be expected. Unfortunately, despite the relatively small area, the available resources were inadequate to provide the intensity of sampling required to answer the questions completely. The results, however, do represent a step forward towards that objective.

THE AREA

The Faroe Islands are situated in the North Atlantic between 62°24′N and 61°20′N and between 6°41′W and 6°05′W. The group, comprising 17 large islands and several small islands and rocks together covering an area ca. 1,400 square kilometres, stands on a submerged plateau which forms part of the ridge connecting Scotland and Iceland. The plateau slopes fairly evenly from a depth of about 50 metres to about 200 metres and from there abruptly to a depth of 300 metres. The 50-metre contour runs fairly close to the islands, the sea bottom continuing the steep declivity of the land down to this depth. The Faroe plateau, which has been taken as being bounded by the 200-metre contour, is roughly triangular in shape with its base to the north and its apex to the south. Off the east side of the islands there are two major banks with depths of around 160 metres and these are separated from the rest of the plateau by narrow channels of deeper water. These have been included in the total area of sea surface of the

plateau, which amounts to 23,300 sq. kilometres. A considerable trawl fishery, largely for cod and haddock is pursued within the area, almost exclusively by Scottish and English vessels. In 1951 the Scottish haddock landings from Faroe—roughly half of the total haddock landings from the area—were 138,729 cwts.

MATERIAL

The material consists of a series of plankton samples collected on a variable number of cruises in each of the years 1950–1953, from some forty stations more or less evenly spaced over the Faroe plateau. The station grid was worked during the periods shown in Table I.

TABLE I

Periods in which Faroe Area was Sampled 1950–53

1950	1951	1952	1953
		February 11–18	February 11–17
		March 14–21	
April 1–19	April 25–May 4	April 6–17	April 6–15
May 14-22	May 20–31		
June 18–27		June 9–21	June 13–20
July 21–August 3	July 15–23		

At each station samples were taken with a Hensen net and a 2-metre ring net hauled vertically from bottom to surface. The Hensen net was made of bolting silk with 60 meshes to the inch, the 2-metre net of bolting silk with 30 meshes to the inch. The bulk of this paper is based on the material from the two nets, the Hensen catches being used for estimating eggs, and larvae up to a size of 8 mm, and the 2-metre catches for larvae above this size. In addition occasional samples were taken with 1-metre townets and with 1-metre high-speed nets (Sheard 1941) to test the validity of the other samples and to provide additional material. In the laboratory no sub-sampling was resorted to, all eggs and larvae being extracted from the rest of the plankton and counted.

SEPARATION OF COD AND HADDOCK EGGS

Experienced workers have accepted for a long time that in early stages of development cod and haddock eggs cannot be distinguished. Statements to this effect are to be found, for example, in Heincke and Ehrenbaum (1900) amongst earlier workers and in Walford (1938) amongst later workers. In later developmental stages whenever the embryo begins to show the pigmentation pattern characteristic of the planktonic larval stage, the eggs of these two species can be separated with ease. In the early stages of development of the two species, however, only the diameter of the egg is available as a characteristic for identification. Although the range of size of the two species is different, 1·26–1·67 mm for haddock and 1·16–1·60 for cod, size can rarely be used directly for specific identification because of the wide overlap. Such a situation severely limits any study of the planktonic stages of these two species in areas where mixed spawning products are to be expected. At the temperatures normally prevailing at the height of the spawning season the eggs will have been subjected for some ten days before identification can be established to the spatial dispersal and mortality, which are the inevitable result of planktonic existence.

Although it would seem impossible to identify, with existing techniques, any individual egg as cod or haddock from a mixture of the eggs of these species, most of the demands of ecological investigations would be met if in a mixed sample one could state the proportion of cod to haddock. If the size frequency

of the eggs of the two species is normal and their means are significantly different, then in any mixed sample the percentage of each species can be found from the point of inflexion of the sigmoid curve obtained by plotting the size frequency of all eggs on probability paper (Harding 1949). To test whether the assumptions underlying this technique are valid, all the cod and the haddock eggs in the samples from one cruise, whose species could be identified on the basis of their pigmentation, were measured under a binocular microscope with eyepiece micrometer. Table II gives the frequency distributions of each species and the relevant statistics.

TABLE II

Size Distribution of Cod Eggs and Haddock Eggs at Faroe, April, 1950

Diameter in micro.-div.	4·7	4·8	4·9	5·0	5·1	5·2	5·3	5·4	5·5	5·6	5·7	5·8	5·9	n	$\bar{x}$	S.D.	g_1	sg_1	g_2	sg_2
Cod eggs ..	8	10	27	33	25	22	11	12	1					149	5·06	0·188	0·172	0·199	−0·542	0·325
Haddock eggs ..				2	10	13	19	50	33	25	13	3	2	170	5·44	0·175	0·069	0·186	0·024	0·370

$\bar{x}_h - \bar{x}_c = 0{\cdot}38 = \bar{d}$

$s_{\bar{d}} = {\cdot}0204$ t = 18·6 P < ·01

The difference between the mean size of the two species is highly significant. To test for normality the statistics g_1 and g_2—measuring skewness and kurtosis—were calculated for each population (Fisher 1954) and their departures from zero tested for significance. As none of the values is significant, we may assume the distributions are normal. Seven such sets of data, covering the cruises over the four years and comprising a total of some 3,000 eggs of each species, have been tested and gave non-significant values of g_1 and g_2. It is also worthy of note that a number of tests of differences between means of the same species at widely separated stations on the same cruise have shown no significant size differences although differences between cruises are always significantly different.

Accordingly the diameter of all cod/haddock eggs has been measured on all cruises and the resulting frequency distributions have been plotted on probability paper. The points of inflexion of the resulting sigmoid curves can generally be fixed fairly accurately by inspection but to get an accurate fix the precise position of the two lines representing the two constituent populations can be adjusted until the best fit to the observed data is obtained.

SPAWNING SEASON

The haddock spawning season is generally accepted as occupying the period January to May. Schmidt (1909) speaking of the haddock spawning at Faroe says, " . . . according to our investigations it falls mainly in April and May". The conclusion to be drawn from the present data is that the spawning season at Faroe is more restricted than the first period and rather earlier than believed by Schmidt. Little if any spawning occurs before March and it tails off rapidly in May. A complete survey of the Faroe area was made in 1952 from 11th–18th February, during which no haddock eggs at all were taken. In the same year the area was again surveyed from 14th–21st March. On this cruise haddock eggs in early stages of development were moderately abundant but no eggs were taken which could have been more than twelve days old. It can be concluded, therefore, that spawning in 1952 was negligible prior to 1st March. A similar conclusion is reached from consideration of the size of the largest larvae taken in April, when the area was sampled in 1950, 1952 and 1953. In 1950 the largest larvae, taken on April 17, were 7 mm long. As is shown on page 16, these larvae would be about 44 days old, which would place the beginning of spawning in that year at 4th March. Similarly the largest larvae in April 1952—again of 7 mm—were taken on 9th April, which would place the beginning of spawning in that season on 24th February, while in 1953 the record of a 6 mm larva on 8th April suggests that spawning in that

year started on 1st March. It is not claimed that these dates accurately measure the commencement of spawning and its variations from year to year, but it is clear from all these data that in none of the four years in which the area has been surveyed did any significant spawning take place before March.

The end of the spawning season can be deduced in a similar way from the stage of development of the youngest forms taken on the June cruises. On this basis spawning was effectively over by the 12th May in 1950, 12th May in 1951, 21st May in 1952 and 8th May in 1953. These figures are sufficiently consistent for it to be said with some degree of confidence that the haddock spawning season at Faroe does not extend beyond the middle of May, and this conclusion is confirmed by the condition of the gonads of haddock taken in the trawl on these cruises. Only one spent haddock has been recorded from March trawl hauls at Faroe, the bulk of the haddock in March being mature or ripe. Spent haddock made up more than half of the adult fish on April cruises, the rest being ripe. On May cruises on the other hand, only nine ripe haddock were taken in the trawl catches; all the other adult fish were spent.

Complete surveys of the Faroe plateau have been carried out in the following periods during the spawning season: April 1–19, 1950; April 25–May 4, 1951; March 14–21 and April 6–17, 1952 and April 3–15, 1953. A convenient measure of spawning intensity during the period of a cruise is the mean number of eggs spawned per day under a standard area of surface. The method of assessing this parameter is given in a later section (p. 16). When these values are calculated for the cruises listed it is clear that spawning does not take place at a uniform rate throughout the spawning period. The values for the cruises centring around the 10th April are fairly consistent at 7·09 eggs per square metre per day for 1950, 8·23 for 1952 and 6·41 for 1953. On the 1951 cruise, centring around the 30th April, the value is only 4·3, while for the March cruise in 1951 it was still less at 1·5. The evidence, inadequate as it is, would seem to suggest that the spawning intensity rises rapidly to a peak around the end of the first week in April and falls off rapidly thereafter. Commercial landing statistics bear out that the peak of spawning occurs in April. It is generally accepted that during the spawning period aggregation of spawning fish occurs on the favoured spawning grounds leading to peak catches. The following mean monthly catches for Aberdeen trawlers at Faroe (Table III) show clearly a peak value in April in 1950, 1951 and 1952 but not in 1953. Data for English* catches show essentially the same picture, even in 1953, when the May value was a little less than that for April.

TABLE III

Mean monthly catch of Haddock—cwt per 100 hours fishing.

Year	March	April	May
1950	140	257	127
1951	140	231	134
1952	126	143	116
1953	107	110	143

The high Aberdeen value for May in 1953 possibly has its explanation in economic or meteorological factors. There is no evidence from the biological data that the peak spawning intensity was later in that year than in the others sampled, and it seems that the value for April 1953 may have been artificially depressed.

SPAWNING AREAS

The limits of the spawning areas of a fish species are usually determined by two methods: (1) from the location of capture of mature fish in quantity; (2) by charting the distribution of the young stages of

* We are indebted to our colleagues at the M.A.F.F. Fisheries Laboratory in Lowestoft for the necessary statistics.

the species in question. The first method doubtless gives a useful rough picture but, since fish may be mature for some time before the spawning act occurs, and may range widely from the final spawning locus, this method tends to give a picture of fairly uniform spawning over wider areas than other evidence would support. Moreover, where factors other than fish density control the location of fishing, important spawning centres may be missed by this method. The second method would seem to give a more direct and accurate picture, provided that the abundance is measured of a stage sufficiently early to minimise the effect of the mass transport and dispersion which operate on any concentration of plankton organisms.

In this investigation the distribution of eggs up to the first appearance of the embryonic axis, i.e., up to about four days old, was used to delimit the spawning areas.

As stated by Schmidt (1909), eggs of the haddock are to be found practically everywhere around Faroe. The density distribution is, however, far from uniform; on every cruise there were three or four centres of high density outside which the numbers taken were small. These centres of egg abundance were remarkably constant from year to year (Figs. 1–4). The area situated to the north of the islands, lying north of 62°30′N and between 6°30′W and 7°30′W, was clearly marked in April of all four years whilst that covering the Nolso Bank—Fuglo Bank* grounds and the grounds to the west of Myggaenaes* were clearly demarcated in each year except 1951, when the survey was too late to sample the main spawning peak (p. 4). In that year a small concentration occurred on the eastern edge of the Nolso Bank where in other years eggs were taken only in extremely small numbers. In 1952 a concentration of eggs occurred to the south of the islands, on the Munken Rock* grounds where in the other years eggs were not abundant.

Even within those spawning loci, which were fairly constant from year to year, certain annual variations occurred in their extent and relative importance. While in 1950 the northern centre was of greater extent and of higher egg density than that of the Nolso–Fuglo region, in other years the latter was the more important. The greatest variability, however, was shown by the spawning centre west of Myggaenaes. In 1952 (Fig. 3) a dense egg concentration covered a wide area in this region; in 1950 (Fig. 1), although the peak concentration here was high, its extent was small; whilst in 1953 (Fig. 2) a rather lower egg density covered a wide area.

The catches of haddock (expressed as cwt per 100 hours fishing) by Aberdeen trawlers during the month of April are plotted on the same charts. It will be seen that there are two main centres of fishing activity in this month, one to the north of the islands and the other on the Nolso–Fuglo Bank region. The location of trawling activity on the Fuglo Bank grounds was fairly consistent in the years 1950, 1951 and 1953; the catches were generally high and the area of fishing coincided with the spawning area as delimited by the distribution of eggs. In 1952 fishing was more intensive nearer the islands, though catches were generally lower than offshore, and the correspondence between the location of the higher catches and the distribution of the eggs is again fairly close; the position is somewhat less distinct to the north of the islands. In 1950 fishing in that area was at a level comparable with that on Fuglo Bank and the correspondence between the higher catches and the egg distribution is quite close. In the other years the exploitation of these grounds was less intensive and the fishing tended to take place closer to the islands and farther east. The resulting catches were lower than those of 1950 and corresponded much less with the egg distributions. The greatest discrepancy between the centres of fishing activity in April (Figs. 1–4) and the areas of greatest egg abundance may have been due to a lack of trawl catch data for this month to the west of the islands. A certain amount of trawling occurs to the south-west of Sydero but only a few vessels are engaged and the catches of haddock are small in comparison with those to the north and east of the islands.

No records of catches from the Myggaenaes grounds in April are available from which the density of haddock on this ground can be measured, and ships which had operated on this ground in April had in all cases been fishing also on other grounds during the trip, so that one cannot allocate the contribution to the total catch made by the different grounds. It may well be that this area holds a concentration of

*Indicated in Fig. 1.

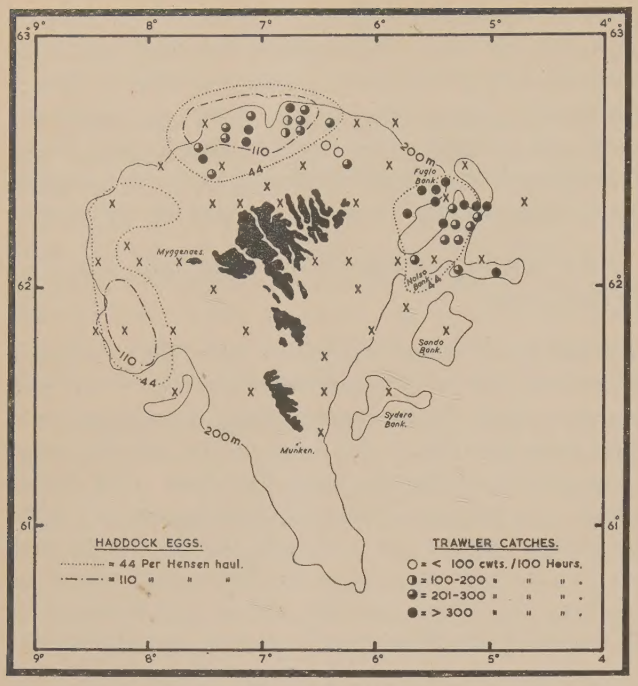


Fig. 1 Distribution of Haddock Eggs and the catches of Haddock by Aberdeen trawlers at Faroe in April 1950.



Fig. 2 Distribution of Haddock Eggs and the catches of Haddock by Aberdeen trawlers at Faroe in April 1951 (Symbols as in Fig. 1).



Fig. 3 Distribution of Haddock Eggs and the catches of Haddock by Aberdeen trawlers at Faroe in April 1952 (Symbols as in Fig. 1).



Fig. 4 Distribution of Haddock Eggs and the catches of Haddock by Aberdeen trawlers at Faroe in April 1953 (Symbols as in Fig. 1).

spawning haddock whose exploitation is rendered difficult by the nature of the bottom or by the exposure of the grounds to bad weather. On the only occasion on which the Faroes were visited in March (1952) there was no sampling to the south-west of the islands. As previously mentioned, spawning intensity on this cruise had not reached a very high level; there was little evidence of spawning activity to the north of the islands but the Nolso Bank centre was active. This centre coincided fairly well with the centre of greatest fishing effort and of the heaviest catches for the month. Such fishing as occurred to the north of the islands was centred farther east and closer inshore than the region delineated as an April spawning centre, and catches of haddock were at a low level. The distribution of later developmental stages as revealed by the April cruises produces evidence that spawning to the north of the islands may begin later than on the southerly grounds (Figs. 6–9). Thus, in 1950, patches of advanced eggs and early larvae were present in the Nolso Bank region southwards to Sydero and to the west of the islands. These can be ascribed to the Fuglo Bank and Myggaenaes spawnings, but there were no patches of these stages which could be easily related to a northern spawning.

Similarly, in all other years except 1951, the only patch of larvae, that could most logically be ascribed to the Fuglo–Nolso Bank spawning and the spawnings to the west and north of the islands, would seem to have been spawned only a short time previous to the April cruises. The position in 1951 was rather different, but this can be explained from the late sampling in that year.

DAY AND NIGHT VARIATION IN CATCHES OF LARVAE

The presence of a diurnal variation in the numbers of planktonic organisms is common in samples taken with any type of horizontal gear and its implications have been discussed by workers with Plankton Recorder material (Rae and Fraser 1941, Marshall 1948). More relevant to the present investigation are the much greater catches of fish larvae taken by night than by day in a series of horizontal hauls sampling different depth strata by Russell (1926) and in vertical hauls by Bridger (private communication). In view of the results of these two workers it seemed imperative to ascertain whether there was any such effect in the present material before using it to study larval distributions.

The stations were accordingly divided into those worked during daylight and those during darkness and the larvae taken in each group of hauls summed; hauls taken during twilight were neglected. As night hauls were markedly fewer than daylight hauls the number of larvae in each group was reduced to the number per station (Table IV). The larvae were divided into four size groups, as it would be expected that, if a variation occurred, it would be most marked in the largest and most mobile larvae. The number of stations was larger in the first size group than in the others because of the inclusion of the April cruises during which none of the larger larvae was present in the samples.

TABLE IV

Haddock Larvae taken on all Cruises in Years 1950-1953 at Faroe

Size Group	Night		Day	
	Total Number	Number per Station	Total Number	Number per Station
3– 6 mm	453*	4·1	810*	3·3
7–10 »	44†	0·88	167†	1·2
11–14 »	33†	0·60	101†	0·74
>14 »	35†	0·70	80†	0·60
No. of Stations	*111†50		*243†137	

Although the numbers per haul varied somewhat between day and night, in no case were the variations of the magnitude that other work on the subject would lead one to expect. The numbers per night stations were larger than the day stations in two cases, and smaller in the other two. Moreover, the largest variation occurred in the smallest size group which is the reverse of what would be expected if diurnal variation were to be explained on the basis of net evasion.

The highly significant differences between day and night catches of fish larvae found by the two authors quoted would seem to be explicable on only two grounds: either (1) that the bulk of the larval fish are distributed in daylight in a narrow layer perhaps too close to the bottom to be fished by the gear used, and that they migrate upwards in darkness within the range of the nets, or (2) that they are able to see and evade the net in daylight. Regarding the first explanation, it is perhaps significant that in the case of both these authors' work the material came from water of less than 60 metres in depth. It may be that the optimum daylight conditions for the fish larvae concerned are situated about this depth. In the case of the present material which was mainly taken in depths of about 150 metres, the larvae would then still be within the depth fished and so the diurnal effect would not be detected. On the second hypothesis no satisfactory explanation for the absence of the effect in this material can be suggested. On the basis of the present material it can only be said that there is no evidence that larvae were able to evade the net significantly during daylight, and that any day and night catch variations, which may have occurred, were not sufficiently large to affect the interpretation of the material significantly.

DISTRIBUTION OF LARVAE IN TIME AND SPACE

Unfortunately, the cruises were in all years too widely spaced in time to attempt to trace the detailed drift of eggs and larvae from the spawning loci. With at least three major spawning centres in such a circumscribed area, the tendency towards dispersion inherent in a planktonic mode of life results in a more or less uniform distribution around the islands. The type of larval distribution, however, found in June can probably best be explained by an anti-cyclonic eddy system around the islands as postulated



Fig. 5 Distribution of Haddock Larvae at Faroe in June 1950-53. The symbols represent the catches of a 2-metre ring net hauled vertically from bottom to surface.

by Tait (1934) for this area (Fig. 5). It would seem necessary to postulate such a system in any case to explain the retention of the haddock spawning products within the area and, with the possible exception of 1950, there is no evidence to suggest that there is any appreciable loss of these products by drift out of the area. Larvae were very scarce in June 1950, and in a later section it is shown that there was a heavy apparent mortality in all stages between the May and June cruises. It will also be noted that those larvae which were taken in June of 1950 were found towards the edges of the shelf surrounding the islands. Again, the westerly wind component in June of 1950 was much stronger than in the other years considered. As the bulk of the larvae in May of that year was already concentrated on the eastern side of the islands it is possible that the prevalence of winds from the west in June resulted in their being carried over the deep water to the east and so lost to the area.

As mentioned in an earlier section, the area, when sampled in March, yielded no haddock larvae. Haddock larvae are, however, to be found in the Faroe region from April to July. These range from newly hatched larvae (3·5 mm) to a size of 7 mm in April, from newly hatched to about 16 mm in May, and from 5 mm to about 30 mm in June. The last size probably reflects the limitations of the gear used rather than a true representation of the maximum size of larvae present. Although larvae of a larger size than this have been taken on occasions, it is not thought that they are representatively sampled above a size of 25 mm with the two-metre net; for example, larvae up to 40 mm have been taken with high-speed nets in June. The area was sampled in July only in 1950 and 1951. In the former year only one haddock larva was taken, at a size of 30 mm; in the latter four were captured ranging from 32-55 mm. The explanation of this is not clear, because from the lower size limits of larvae in June, one would expect to find larvae around 15 mm still present in the area in mid-July. It is unfortunate that the area was sampled in July only in these two years, for there is other evidence to suggest that the products of the later spawning in 1950 met an untimely end and, as there was no sampling in June of 1951, the July observations are rather isolated in time. The area, however, was sampled by horizontal one-metre townets in July 1949 in the course of other work. On that occasion considerable numbers of haddock larvae ranging in size from 16 mm to 47 mm were taken. It would accordingly appear that the extreme paucity of larvae in July of 1950 and 1951 might be a peculiarity of those two years rather than a normal feature of the seasonal cycle.

In April the bulk of the larvae present was found on the east side of the islands (Figs. 6–9). In 1952 and 1953 the only larvae taken in this month were off the east coast of Faroe, in the Nolso Bank region, and in 1950 and 1951 the largest concentrations were also on the east side although somewhat farther south. In the latter two years, however, there were other patches, i.e. on the west side of Sydero in 1950 and to the north of Fuglo in 1951. It would appear that in all years the major patch of larvae in April could be ascribed to the spawning on the Fuglo and Nolso Banks from which it would follow that in 1950 and 1951 the drift was south-westerly and at about the same speed in both years, whilst in 1952 it was south-easterly and in 1953 it was southerly and at a slower speed.

The Faroe area was sampled in May only in 1950 and 1951. In these two years the distribution of haddock larvae was entirely different (Figs. 10–11). In 1950 they were present in two distinct patches but almost entirely to the east of the islands. One patch covered the north-east corner from Enniberg to Fuglo Bank whilst the other extended from Nolso down the east side of the islands and around the south of Sydero. In contrast, they were present in 1951 as a presumably discrete patch extending from the west of Sydero all along the west side of the islands and along the north coast.

GROWTH

The interpretation of larval fish material is greatly facilitated if definite ages can be ascribed to larvae of different sizes. To do this requires the calculation of growth coefficients. In adult fish this can be done by following the advance of the modes of homologous groups. Owing to the prolonged spawning period and the high mortality, this is rendered difficult in the larval stages; during most of the season the smaller sizes are so predominant numerically that the larger do not form distinct modes but are evident



Fig. 6 Distribution of Haddock Larvae at Faroe in April 1950.



Fig. 7 Distribution of Haddock Larvae at Faroe in April 1951 (Contour levels as in Fig. 6).



Fig. 8 Distribution of Haddock Larvae at Faroe in April 1952 (Contour levels as in Fig. 6).



Fig. 9 Distribution of Haddock Larvae at Faroe in April 1953 (Contour levels as in Fig. 6).



Fig. 10 Distribution of Haddock Larvae at Faroe in May 1950.



Fig. 11 Distribution of Haddock Larvae at Faroe in May 1951 (Contour levels as in Fig. 10).

chiefly as the lengthening of the tail of an arithmetic frequency distribution in the higher sizes. The difficulty can be overcome when cruises follow sufficiently closely during the planktonic phase by adopting the technique described by Sette (1943). His method is not completely satisfactory on two counts. Firstly it gives no basis on which to assess a standard error with which to test the significance of modes, thus allowing the possibility of selecting false modes due to sampling variation; secondly a certain amount of latitude is allowed for personal bias in selecting homologous modes and other criteria are needed to ensure that the choice made best fits all aspects of the data. In the present work this technique is rendered even less satisfactory owing to the fact that even in the best year (1950) there were only three cruises during the period when larvae were to be found. With the limited data available however no better method is available, and accordingly the technique has been applied to the data for 1950 and confirmation of the derived coefficient obtained from its compatability with other data.

The method is essentially a modification of the conventional "deviation from the average frequency" technique. The average numbers per cruise of the larvae in each size group are converted to their logarithms and plotted against the logarithms of the corresponding lengths (Fig. 12). Larvae over 8 mm in length are grouped into 5 mm size groups. Straight lines are fitted to these points and from them the theoretical values of Table V are derived.

The theoretical log values are then subtracted from the corresponding individual cruise values to give a measure of the amount by which the larvae of each size group on each cruise deviate from the average for all cruises—an operation which effectively gives a measure of their frequency after elimination of mortality effects. The deviations for each cruise are then plotted against the logarithms of the corresponding lengths. The choice of homologous modes is primarily governed by the assumption that growth would be exponential, as Sette has shown best fits the data for growth in other young fish. Three lines have been drawn through homologous modes, lines a, b and c, giving growth coefficients of 0·012, 0·011, and 0·012 (Fig. 13). This is in substantial agreement with Walford's (1938) Fig. 50 from which a growth

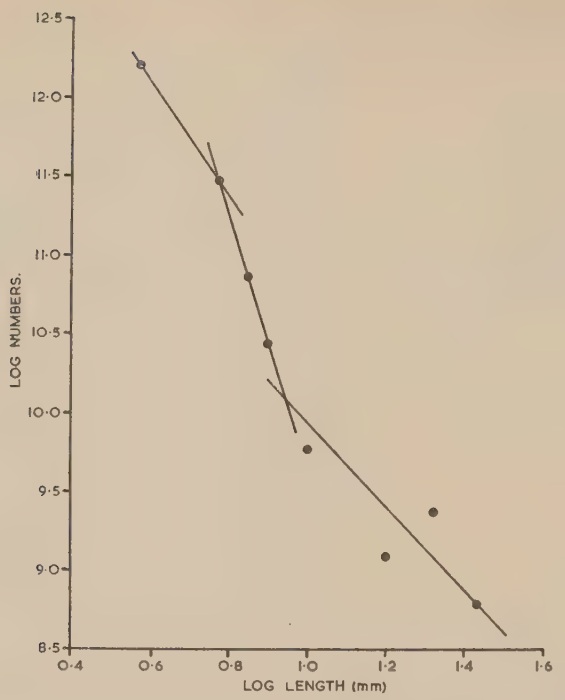


Fig. 12 The average number per cruise of Haddock Larvae in each size group at Faroe in 1950, plotted logarithmically (See page 12).

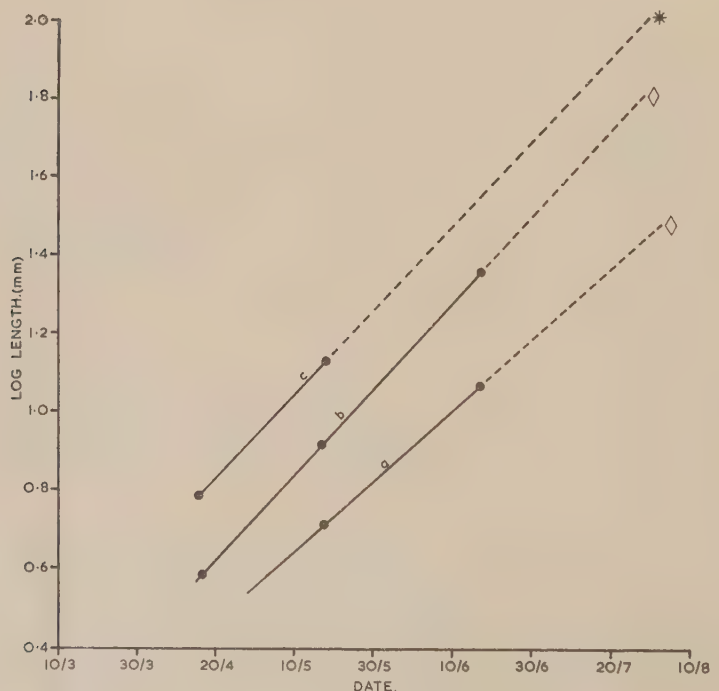


Fig. 13 Growth of Haddock Larvae at Faroe in 1950, as derived from the progression of homologous modes. The sizes of pelagic larvae taken in July and August are denoted by diamonds and the size of the largest 1950 brood Haddock taken in the trawl on this cruise by an asterisk (see page 15).

TABLE V

Deviations of Individual Cruise Frequencies of Lengths of Larvae from Average Frequency of the Three Cruises of 1950

Length		Average No. per Cruise			Cruise Deviations (Log)		
mm	log	Observed Values		Theoretical Value (Log)	1	2	3
		Number	Log				
3·75	0·574	158	12·20	12·20	+0·27	+0·05	—
5	0·699	48	11·68	11·72	+0·06	+0·17	—
6	0·778	29	11·46	11·46	−0·26	+0·38	—
7	0·845	7·7	10·89	10·90	−0·28	+0·36	—
8	0·903	2·6	10·42	10·41	—	+0·48	—
9	0·954			10·06	—	+0·14	—
10	1·000			9·93	—	+0·27	—
11	1·041	0·57	9·76	9·81	—	+0·39	−0·09
12	1·079			9·71	—	+0·39	−0·23
13	1·114			9·62	—	+0·58	—
14	1·146			9·53	—	—	−0·05
15	1·176			9·44	—	+0·34	+0·04
16	1·204	0·12	9·08	9·36	—	+0·12	+0·12
17	1·230			9·29	—	—	—
18	1·255			9·23	—	—	—
19	1·279			9·15	—	—	+0·63
20	1·301			9·10	—	—	+0·37
21	1·322	0·23	9·36	9·05	—	—	+0·73
22	1·342			8·98	—	+0·58	+1·13
23	1·362			8·93	—	—	+0·45
24	1·380			8·88	—	—	+0·60
25	1·400			8·83	—	—	—
26	1·415	0·06	8·78	8·78	—	—	+0·70
27	1·431			8·73	—	—	—
28	1·447			8·68	—	—	—

coefficient of 0·0115 can be deduced. These lines of exponential growth are admittedly based on too few points to give great confidence in them by themselves. They do, however, derive a certain confirmation from other data. The July survey in 1950 yielded too few pelagic larvae to allow of their being incorporated in the graphs directly. The two caught, however, on the 29th July and the 3rd August respectively measured 30 mm and 60 mm. These are shown as diamonds on Fig. 13 where it can be seen that they agree fairly well with the projection of the b and c curves to these dates. During the same survey a considerable number of small haddock of the 1950 brood were taken in the small mesh cover of the trawl. These ranged in size from 4 to 10 cm. If the c curve is projected to the date of this cruise it gives a size of 10 cm for the largest larvae obtainable at this date. This sort of agreement engenders more confidence in the growth coefficient than the original data can do alone.

The same technique has been applied to the total material from all the surveys over the four years. Cruises in different years occurring within a few days of each other have been grouped and the mean of each size group taken. This procedure has resulted in four deviations from the average frequency curves. The straight line joining the most consistent group of modes gives a growth coefficient of 0·0118.

Another approach to the problem is to split the size frequency distribution of the larvae from each cruise into its constituent normal distributions, using the probability paper technique. This method is not completely satisfactory without a knowledge of the number of constituent populations involved in each distribution but it provides some confirmation of the conclusions derived by the other methods.

The theoretical frequencies for each cruise so derived are tested for goodness of fit against the observed frequencies by means of a χ^2 test, the lowest probability being 0·1. The logarithms of modes of the constituent distributions are then plotted against time and straight lines drawn connecting the modes for the same years. In this way four straight lines were obtained giving coefficients of growth of 0·012–0·013. The agreement between the figures obtained by these methods is probably as close as could be expected from the nature of the material. More accurate assessments from which variations in growth within a season and between seasons could be estimated would require throughout a season cruises at much more frequent intervals than has been possible. From the present data, however, it can be stated that the best available estimate of the coefficient of growth of Faroe haddock larvae is an increase of 0·012 per day in the logarithm of the length.

One of the main applications of this growth coefficient is in the calculation of the average age of a size group and the average life of a group, both of which are necessary in mortality estimations. The average age of a category is obtained from the formula $\frac{L-l_1}{0{\cdot}012}+13{\cdot}5$ where L is the mid value of the size group, l_1 is the size of new hatched larvae and 13·5 is the age in days at hatching. The life, or duration, of a category by the same reasoning is $\frac{l_3-l_2}{0{\cdot}012}$ where l_3 is the upper limit of the category and l_2 is the lower limit of the category.

ESTIMATION OF ANNUAL EGG PRODUCTION

The problem of estimating the total number of eggs spawned within an area from a series of cruises spaced throughout the spawning season has been fully discussed by Sette and Ahlstrom (1948). It is essentially the integration of the data from each cruise over space and of all the cruises over time. The cruise data consist of counts of haddock eggs from Hensen hauls for the various stations. For estimating egg production only eggs up to ten days old, as defined by Dannevig (1898) and Apstein (1909), are used. The net numbers are converted to the numbers of eggs per 1 m^2 of surface by multiplying by 2·6. This assumes that the Hensen net filters the theoretical quantity of water—an assumption which probably leads to no serious error in this area as the phytoplankton crop at Faroe is never sufficiently dense at this season to cause any appreciable clogging of the silk. These then represent the accumulation of eggs over eleven days; accordingly the figure for each station is then divided by eleven to give the number of eggs spawned per day below each square metre of surface for that station.

It is now necessary to integrate these observations over space to give an estimate of the total spawning per day for that cruise over the whole area. Two approaches to this problem seemed to offer themselves, either to weight each station according to its distance from adjacent stations, or to give all stations equal weighting. Sette and Ahlstrom, in adopting the first technique, constructed a system of polygons each enclosing one station and weighted their station observations according to the proportional areas of the polygons. This technique was tried on the data from the first year. It was found, however, that the answer so obtained differed little from that derived by weighting all the stations equally and the labour involved in introducing this refinement seemed unjustified in view of the station grid occupied and the other and more serious sources of error. Accordingly the technique finally adopted was to multiply the mean number of haddock eggs spawned per square metre per day by the area of the Faroe plateau within the 100 fathoms contour (2331×10^7 m^2).

The next problem is to integrate these cruise observations over time. Sette and Ahlstrom assumed that the egg concentrations observed during a cruise represented not only that cruise but also an adjacent

period of time equivalent to half the period between that cruise and the preceding one plus half the period between that cruise and the following one. This method probably gives a fairly satisfactory approximation where, as in their material, six cruises are spaced throughout the spawning period and the inter-cruise periods are fairly short. Even so, they had a period prior to their first cruise for which an estimate had to be made from the numbers of larvae taken on the first cruise. In the case of the present material, where the cruises are widely spaced (and indeed in some years only one cruise is available to characterise the spawning period), this method is not very satisfactory—it entails the assumption that spawning is at a constant rate over a longer period than the data give any reason to suppose is justified. Moreover, there remains at the beginning or end of the spawning season an indeterminate period which can only be assessed from the density of the resulting larvae by making some sort of assumption about the rate of mortality. This technique can perhaps be most satisfactorily applied to the 1952 data. The assessment for that season on this basis is set out below.

First cruise 14th–21st March. Period of cruise 6th–28th March $=23$ days.

Mean number of haddock eggs per square metre for 1st cruise $=15{\cdot}9$.

These are the accumulation of eleven days' spawning.

$\therefore$ the mean number of haddock eggs per square metre spawned per day $=\frac{15{\cdot}9}{11}=1{\cdot}45$

On this cruise the whole area was not surveyed. The area of surveyed portion was 1282×10^7 m^2

$\therefore$ total spawning assessment for period of the cruise for the surveyed area $=23\times1282\times10^7\times1{\cdot}45$
$=4275\times10^8$

From the relative amounts of spawning in the surveyed and unsurveyed portions on other cruises this figure must be multiplied by 1·17 to compensate for the unsurveyed portion.

Then total spawning for period of cruise for the whole area $=50\times10^{10}$.

Second cruise 6th–17th April. Period of cruise 29th March–25th April $=28$ days.

Mean number of haddock eggs per square metre for 2nd cruise $=90{\cdot}48$.

These are the accumulation of eleven days' spawning.

Then mean number of haddock eggs per square metre spawned per day $=\frac{90{\cdot}48}{11}=8{\cdot}23$.

The total area of the plateau $=2331\times10^7$ m^2.

Then total spawning assessment for period of the cruise for whole area $=28\times8{\cdot}23\times2331\times10^7=537\times10^{10}$.

As was stated on page 6, spawning continued until 14th May and there is no cruise sampling for the period 25th April–14th May from which to estimate the spawning during this period. This can only be estimated from the frequency of larvae on a later cruise, which were spawned during this period, relative to the frequency of larvae of a similar size spawned during one of the periods sampled for eggs.

Eggs spawned on 26th April are estimated to be 8 mm in length by 12th June. Larvae of this size on the April cruise were spawned during the March cruise.

The number of 4–8 mm larvae on the June cruise/number at this size on the April cruise $=0{\cdot}1$

Then the mean spawning rate per day for the period

$$26\text{th April–14th May}=\frac{1{\cdot}45}{10}$$
$$=0{\cdot}145$$

Then spawning assessment for the period
$=19\times2331\times10^7\times0{\cdot}145$
$=6\times10^{10}$

Spawning began on 1st March (p. 6) and again there was no cruise to sample the eggs present during the period 1st–6th March. These can best be assessed from the relative numbers of late eggs on the March cruise, which must have been spawned during this period, to late eggs on the April cruise which were spawned during the first cruise. This rate is 0·04.

Then the spawning rate per square metre per day for period 1st–6th March $=1{\cdot}45\times0{\cdot}04$
and the total spawning assessment for this period for whole area $=5\times2331\times10^7\times1{\cdot}45\times0{\cdot}04$
$=1\times10^{10}$

so that the best estimate of total spawning for the season $=59\times10^{11}$.

It should be noted that the estimates of spawning prior to the first cruise and following the April cruise are based on the assumption that mortality was constant for advanced eggs between March and April and for 4–8 mm larvae between April and June. As will be shown later there is reason to think that mortality rates may vary considerably within a season so that this assumption may cause a considerable error. In this instance the contribution to the total made by these two periods is in any case too small to affect the total significantly.

In other years, when the cruise spacing was even less satisfactory, this method cannot be adopted without making even more far-reaching assumptions about mortality rates. The only approach in these

cases would seem to be to make some assumption about the form of the curve of spawning intensity throughout the season from which the total area enclosed by the curve can be deduced from a portion of it. Sette and Ahlstrom assumed for their data that the distribution between cruises was linear but do not discuss the shape of the spawning curve for the season as a whole. In the present data there are too few points in any year during the spawning season to define the curve; all the evidence, however, would suggest that the general course of events is for the intensity of spawning to rise from a low level near the beginning of the spawning period to attain a peak towards the middle of it and to drop off again afterwards to a low level towards the end. Under these circumstances the two simplest assumptions are (*a*) that spawning intensity is linear from zero before the beginning of the spawning season to a peak value at the middle of it and again from the peak value to zero at the end of the season; (*b*) that the course of spawning intensity throughout a season follows a normal frequency curve. The latter solution gets a certain measure of support from other data.

The only two papers in which reasonably adequate measures of the spawning intensity of a fish species are available throughout a season are by Sette (1943) and Sette and Ahlstrom (1948). If from Table V in the former, one takes the numbers of Stage A eggs on successive cruises and plots them against the mid-date of the corresponding cruise, a curve closely approximating to a normal curve is obtained, apart from the fact that the left-hand side is incomplete due to lack of data during the early part of the season. If, however, this curve is continued backwards it approaches very close to the axis about the 14th April. In the text the author remarks that spawning of mackerel off the coast of Southern New England begins during the middle of April. These data then would seem to give as good a fit to the normal curve as could be expected considering their nature. Sette and Ahlstrom (1948) supply data for two years. Taking the first column of their Table 1 ($D\Sigma W_i^1 C_{ia}$) and dividing it by the corresponding D one gets a measure of the spawning intensity for each cruise. Plotting these for 1940 against time one gets a curve with a slight bimodality. The original data for this paper (Ahlstrom, 1948) showed that on the two cruises responsible for this appearance of bimodality nine and seven stations respectively were omitted. When the positions of these omitted stations are compared with the distribution of eggs for that season (their Fig. III) it is found that at least three of them were in a region of very high egg density in each case. It would appear probable therefore that the spawning intensity for these two cruises has been underestimated by the authors and that this appearance of bimodality is an artifact due to sampling deficiencies. Turning to the 1941 data and treating them in the same way one obtains a curve which—apart from one point—gives a reasonable semblance to one half of a normal curve. It is clear, however, from subsequent work in this area (Anon, 1952) that the data under consideration are far from complete, covering as they do only a portion of the now known spawning region within which there is a seasonal progression in spawning from south to north, so that it is hardly surprising that these data do not fully support the hypothesis of normal spawning frequency.

As there is nothing in the published data to refute the hypothesis and since there is some slight support for it, this technique has been applied to the present data; it seems likely to give at least a reasonable approximation to the number of haddock eggs spawned in Faroese waters in a season. It was shown in a previous section that all the effective spawning at Faroe takes place between 1st March and 14th May —a period of 75 days. This has been taken as equal to six times the standard deviation of a normal curve. In 1951, when the beginnings of spawning would seem to have started considerably later,* the spawning season was taken as having extended from 14th March-14th May—a period of 61 days.

As an example of the application of this technique the derivation of the season's spawning assessment for the 1950 season is given below.

The spawning season is considered to extend from 1st March–14th May = 75 days; i.e., 75 days is regarded as equal to six times the standard deviation of the spawning curve, so that the standard deviation $= \frac{75}{6} = 12{\cdot}5$.

The mid-point of the range is 7th April, and the period of the relevant cruise is 1st–19th April.

*It is perhaps relevant that the bottom temperatures obtained in the April cruise of 1951 were on the average about 0·5°C less than in the coldest of the other years.

The number of eggs spawned per square metre during this cruise = 135. The normal deviate of the proportion of the eggs spawned between 1st and 7th April = $\frac{7}{12{\cdot}5}$. From a table of normal deviates this is equivalent to 21·23% of total eggs enclosed by the normal curve.

Similarly the proportion of eggs spawned between 8th and 19th April is equivalent to 33·15% of the total eggs enclosed by the normal curve so that the percentage of the total season of spawning between 1st and 19th April is 54·38%. Now 54·38% of total season spawning is 135 eggs per square metre, so that the total spawning for season is 248 eggs per square metre. Therefore, the total number of eggs spawned in the whole area over the whole season $= 248 \times 2331 \times 10^7$
$= 58 \times 10^{11}$.

By the same technique the figures derived for the four seasons sampled are:—

1950	1951	1952	1953
58×10^{11}	70×10^{11}	67×10^{11}	49×10^{11}

It will be seen that the spawning assessment derived in this way for the 1952 season does not differ widely from that found by Sette and Ahlstrom's technique (p. 17). It is now of interest to see how these spawning assessments for the different years compare with the size of the corresponding spawning stocks. Perhaps the best available index of the latter is given by Jones (1951) and Jones and Main (1952, 1953 and 1954), in the form of the catches per 100 hours of Aberdeen trawlers at Faroe. From these tables the mean catch per 100 hours for the months of March and April has been taken as the best index of the comparative density of spawners. In the tables the catch is given in market categories: Extra Large and Large, Medium and Small. Small has been ignored as adding little to the spawning potential. The mean size of Extra Large and Large is 52 cm approximately and of Medium it is 41 cm. The weight of a fish is proportional to the cube of its length and, according to Raitt's (1933) data for North Sea haddock, the fecundity is proportional to $l^{3{\cdot}8}$ (where l = length). On this basis, the fecundity per unit weight of the category XL and L is 1·25 times that of Medium. Applying this factor to the catches per 100 hours for March and April, one gets for the comparative spawning potential of the stocks for these years:—

1950	1951	1952	1953
164	176	140	110

These figures, although not proportionate to the corresponding spawning assessments, are in the same order apart from the small index of fecundity for 1952. A possible explanation of this may be that in 1952 an unusually large proportion of the spawning occurred to the west of Sydero on grounds which are very little fished by Aberdeen trawlers, so that any increase over the years in the spawning stock on the grounds west of Sydero would not show in these data. Such evidence as there is from English trawler landings suggests that spawning was indeed rather higher in that year. Considering all the limitations of the data and the confidence limits indicated below, the agreement is perhaps as good as can be expected.

The question now arises of assessing the reliability of these estimates. There would appear to be three main sources of error in them:—that due to collecting the individual samples, and those due to the method of weighting used in integrating the individual samples over space and the cruise totals over time. As regards the first, during the course of the surveys, duplicate Hensen samples were taken at all stations over one cruise with a view to assessing the variability of a single sample. In deriving the station variance, all samples with less than ten eggs were omitted and a logarithmic transformation of the remaining data was employed. The standard deviation of a single observation as derived from these data was 0·0976—equivalent to a deviation of 25% of the mean. This compares favourably with Windsor and Clarke's (1940) estimate from Künne's data of 47% and Cushing's (1953) estimate of 64% for Hensen hauls. Perhaps the smaller variability found in the present data is due to the fact that the immobile fish-eggs do not tend to collect in localised swarms as do the copepods etc., on which these authors worked. Using this estimate of the standard deviation the 95% confidence limits for a single observation are 63% and 160% and the contour levels used in Figs. 1–9 derived from these limits are 1, 3, 7, 17, 44 and 110 eggs per haul. The application of the variance of a single observation to the estimation of the error due to this source in a season's estimate has been discussed by Sette

and Ahlstrom (p. 527-535). These authors calculated coefficients of variation of 5% and 10% for the estimates of the two seasons they sampled. In view of the smaller haul to haul variance obtained in the present work it would appear that the error due to this source would not exceed 7½% in any season.

In view of the lack of any obvious trend in the station values the best available estimate of the error involved in integrating station values over space to give a cruise total is found from the standard error of the mean. The standard errors of the season's estimates are 9×10^{11} for 1950, 2×10^{11} for 1951, 5×10^{11} for 1952 and 4×10^{11} for 1953. These will be over-estimates of the errors introduced in integrating over space as it is highly unlikely that the distribution is a random one.

Similarly, in interpolating over time the estimate is largely controlled by the assumed dates of beginning and ending of the spawning season. If for example the season started a week earlier in 1950 than assumed, the estimate would be increased by 16%. The evidence for the dates used, however, is sufficiently strong for it to be thought that the error introduced in this way will be fairly small. A more serious error of course would be caused if the assumption of normality were seriously at fault. For example if spawning were linearly distributed the 1950 estimate would have to be increased by about 38%

Another major source of error operating on these estimates is due to the effect of mortality on the eggs. As previously mentioned, the estimates are based on eggs up to 10 days old. This leads to two sources of error:—(*a*) there is an over-estimate due to the inclusion of some eggs which were in fact spawned previous to the period of the cruise and (*b*) the eggs which were spawned during the cruise are somewhat underestimated due to their reduction by mortality during the ten day period. The error due to the inclusion of eggs spawned outwith the period of the cruise can be assessed from the normal spawning curve and does not exceed 5×10^{11} in any of the seasons sampled. As regards the errors introduced by mortality acting on the eggs during their first ten days of planktonic life, if one assumes a daily mortality of 5% (a figure not unreasonable in view of the mortality rates given in the next section), the estimates would require to be increased by 20%.

Applying all these corrections, one gets the following approximate confidence limits for the estimates previously derived:—

for 1950,
58×10^{11} (confidence limits $31\times10^{11}-100\times10^{11}$);
for 1951,
70×10^{11} (confidence limits $56\times10^{11}-102\times10^{11}$);
for 1952,
67×10^{11} (confidence limits $46\times10^{11}-105\times10^{11}$);
for 1953,
49×10^{11} (confidence limits $32\times10^{11}-75\times10^{11}$).

LARVAL ABUNDANCE AND LARVAL MORTALITY

Perhaps of more direct bearing on the question of brood fluctuations are the relative numbers of larval stages at comparable periods in different years. If, as has been suggested by many writers, brood fluctuations are caused by differential mortality at some critical stage in the planktonic phase of the species in question, then a reliable estimate of numbers of larvae surviving beyond this critical stage should give a measure of recruitment for that year brood. Moreover, a more exact definition of this critical stage would be a big step forward to the final elucidation of the whole problem. From the present data we have estimates of the abundance of larvae in all four years for April, for two of the years in May and for three of the years in June. The April and May figures are based on catches by Hensen net, those for June on samples collected by the two-metre net. In all cases the catches are given in terms of the mean number of larvae below 100 square metres of surface. Table VI gives the figures for the April cruise.

TABLE VI

Abundance of late Haddock Eggs and of Haddock Larvae in April.

Stages	1st–19th April 1950	25th April–4th May 1951	6th–17th April 1952	6th–15th April 1953
egg				
IV & V	1097	1019	611	556
4 mm	1451	458	135	224
5 "	159	62	195	52
6 "	38	14	22	10
7 "	13	21	5	—

One thing stands out clearly from this table—the marked superiority in abundance of both advanced eggs and early larval stages in 1950 over all the other years. One possible explanation is that spawning had started earlier in 1950 than in the other years and so passed its peak before the date of this cruise. This explanation would at first sight seem to find some support in the fact that in 1950 a larval stage was more abundant than the late egg stage. It must be borne in mind, however, that to get a true comparison of numbers between stages they must be reduced to the numbers occupying a comparable duration of time. If this is done on a per day basis, the comparable numbers of advanced eggs and 4 mm larvae for this cruise are 274 and 97 respectively, numbers, which on the basis of a moderate mortality, are compatible with an increasing rate of spawning. Other data, however, do not support this explanation; firstly, the largest larva taken on this cruise was only 7 mm long—a size equal to that attained by this date in other years. Moreover, though a complete survey was not carried out in March of 1950, a few stations were worked on the tenth of that month, in which all the main spawning centres were sampled. The numbers of eggs taken in these hauls were low, rather less than were taken at comparable stations in March of 1952, and none was more than ten days old. All the evidence would suggest that spawning in 1950 did not start earlier than in the other years surveyed, but that there was truly a greater abundance of larvae in April 1950 than of the others years. Larvae were also more numerous in 1951 than in the succeeding two years, although since the cruise in that year was considerably later than in the others, it is difficult to assess the significance of this. The differences between 1952 and 1953 are too small to be significant.

The figures for the only two May cruises are given in Table VII.

TABLE VII

Abundance of late Haddock Eggs and of Larvae in May

Stage	14th–22nd May 1950	20th–31st May 1951
Advanced eggs	272	464
4 mm	160	224
5 "	90	150
6 "	54	80
7 "	16	48
8 "	10	35
9 "	3	42
10 "	3	26
11 "	3	19
12 "	3	10
13 "	3	10
14 "	2	6
15 "	1	3
>15 "	1	2

The figures for all stages are larger for 1951 than for 1950, and the difference is most marked in the size range 7–14 mm. These must have been present as advanced eggs and as small larvae in the previous cruise in both years—and as such were definitely more numerous in 1950 than in the succeeding year, and so one arrives at the conclusion that the mortality between the first two cruises was heavier in 1950 than in 1951.

Table VIII gives the corresponding figures for larvae for the June cruises of the three years in which the area was sampled in that month.

TABLE VIII

Abundance of Haddock Larvae in June

Stage	18th–27th June 1950	9th–16th June 1952	13th–20th June 1953
4 & 5 mm	—	15	—
6 "	—	8	0·6
7 "	—	7	—
8 "	—	3	3
9 "	—	5	3
10 "	—	4	4
11 "	2	8	7
12 "	1	6	5
13 "	—	7	9
14 "	1	8	6
15 "	1	10	11
16 "	1	6	9
17 "	—	5	5
18 "	—	2	2
19 "	2	3	3
20 "	1	1	2
>20 "	10	4	6

These June figures should theoretically give the best index of the recruitment to the current year brood. By this month at least the bulk of the larvae ought to have passed any critical stage in their pelagic life. It should also be borne in mind, however, that the earliest spawned larvae will by this time have attained such a size that they will be no longer liable to capture by conventional plankton equipment. Perhaps the most marked discrepancy between these figures for the three years lies in the absence of larvae below a size of 11 mm in 1950. Admittedly the 1950 cruise was somewhat later than those of the other two years but not sufficiently late to account for the difference found. Late stage eggs and small larvae were taken in the May cruise of this year and these should have been present at the appropriate sizes in the June cruise. Their absence can hardly be explained except by postulating a sufficiently heavy mortality to reduce them to such a low level of abundance as to be undetectable by the technique employed. The paucity of larvae of 11–18 mm in 1950 compared with the other two years is also well marked. These must have been spawned during the April cruise when the level of abundance of eggs did not vary very markedly and the 1950 level was intermediate between those of the other two years. For these 11–18 mm larvae also one can only postulate a greater mortality in 1950 than in the other two years. Those greater than 20 mm on the other hand were somewhat more abundant in 1950 than in the other years which would suggest that for those eggs spawned early in 1950 survival was fairly high. The figures for 1952 and 1953 are probably not significently different, above the size of 9 mm at least. Larvae of a lesser size than this were more abundant in 1952 than in 1953. This could be due to a reduced intensity of spawning late in the 1953 season or to a lesser mortality during that period. There is no evidence available to arbitrate between these two possible solutions.

To measure these mortality rates presents some difficulty. Sette (1943) has discussed this problem but his technique demands that the various stages in development be sampled in proportion to their abundance during their entire planktonic phase. These conditions were not met in the present survey. Moreover the mortality rates derived by this method are mean rates for a stage throughout a season and give no measure of variation in mortality of products spawned at different times within a season. With the present material the best course is to attempt to follow homologous groups from cruise to cruise. As an example of the technique, consider the eggs spawned during the first cruise in 1950. Spawning during this cruise was at a mean frequency of 7·09 eggs per square metre per day. The total number of eggs spawned during this cruise then was $7{\cdot}09 \times 19 \times 2331 \times 10^7$. By the May cruise these eggs would be represented by larvae from 25–51 days old (mean age 38 days), that is by one-fifth of the 4 mm larvae and all

the 5, 6, 7 and 8 mm larvae. Of these there were 5·90 per square metre on this cruise. These, corrected for the duration of the category, are equivalent to 2·04 per square metre, so that the total number in the area is equal to $2{\cdot}04 \times 2331 \times 10^7$. Therefore if x is the percentage rate of mortality per day,

$$7{\cdot}09 \times 19 \times 2331 \times 10^7 \left(1-\frac{x}{100}\right)^{38} = 2{\cdot}04 \times 2331 \times 10^7 \text{ and } x = 10{\cdot}5\% \text{ per day.}$$

A similar technique was applied to the data for other stages, and for those other years in which a stage or a group of stages can be followed from one cruise through to a succeeding stage in a subsequent cruise.

In the case of the first cruises of a season the mortality of stages later than early eggs can be estimated if one accepts the hypothesis of normal spawning frequency. For example, on the first cruise in 1950 larvae of up to 5 mm were the dominant larval stage. These were 14-35 days old, i.e. spawned from 1st March to 29th March. On the normality hypothesis 23·58% of the total season's eggs were spawned during this period, i.e. 1367×10^7 eggs provided these larvae. The number of larvae taken in April at these sizes was equivalent to 14·9 per square metre, equivalent to 34474×10^7 over the whole area, giving a percentage mortality per day of 5·36%. The calculated mortalities between different stages for the various years are set out below.

For the 1950 season:—

Newly spawned eggs in March to 4 and 5 mm larvae in April	5·4%	per day
4 and 5 mm larvae April to larvae >7 mm in May	7·7%	„ „
The bulk of these had left the plankton by June.		
Newly spawned eggs in April to 4–6 mm larvae in May	10·5%	„ „
4–6 mm larvae in May to 10–21 mm in June	10·7%	„ „

For the 1951 season:—

Newly spawned eggs in March-April to 4–7 mm larvae in April	16·15%	„ „
4–7 mm larvae April to 6–16 mm larvae in May	3·8%	„ „
Newly spawned eggs April–May to 4 and 5 mm larvae in May	8·6%	„ „

For the 1952 season:—

Newly spawned eggs in March to 4 and 5 mm larvae in April	9·6%	„ „
4 and 5 mm larvae in April to larvae >17 mm in June	4·8%	„ „
Newly spawned eggs in April to 9–15 mm larvae in June	9·5%	„ „

For the 1953 season:—

Newly spawned eggs March to 4–6 mm in April	10·6%	„ „
4–6 mm larvae April to >16 mm larvae June	3·8%	„ „
Newly spawned eggs April to 11–16 mm larvae in June	8·04%	„ „

It will be seen that these mortality rates broadly conform with the generalised deductions made above, viz. that in 1950 the early spawned eggs suffered a much smaller mortality rate than in the other years; that between April and May mortality in the larval stages was much less in 1951 than in 1950; and that larvae of 10–20 mm in June of 1950 had undergone a heavier mortality than the corresponding larvae in the other two years. There is no basis on which one can assess the accuracy of these figures. They would seem to depend on two main factors. First, that all stages were sampled in conformity with their abundance—for example the accuracy of the estimates for the later stages would be seriously affected if there were any significant net evasion for these stages. It is believed that this was not a serious factor. As previously mentioned (p. 10) there was no evidence of a diurnal effect in these stages; larvae of a considerably larger size than those considered here were on occasion taken in appreciable numbers, and finally mortality at the larger sizes was generally less than at the smaller stages. The other main factor on which the accuracy of these assessments depends is the accuracy of the growth coefficient used in deducing the homologous groups (see p. 15). Another point which should perhaps be stressed here is that in this investigation any decrease of larvae in the area has been considered as mortality—whether due to loss through mortality or through drift out of the area.

The cruise spacings were not sufficiently close to give mortality rates over sufficiently short time periods from which to derive accurate conclusion about any critical phase for survival. It will be noted, however, that mortality in general was heaviest (at around 10% per day) in the early stages, i.e. from newly hatched eggs to small larvae. This rate of mortality, however, would seem to be normal for this stage, being markedly exceeded only in the eggs spawned earliest in the season 1951 and significantly less in early spawned eggs in 1950. In neither case does it appear to have had a critical effect on the fate of the year brood. The most marked variation in mortality would appear to have been in a post-larval stage in 1950, when it was more than twice the highest mortality suffered by this stage in other years. It is significant that recruitment of this year brood as measured by the number of O-group haddock caught by F.R.S. *Scotia* at Faroe is only about half of those obtained in the other three years which varied little amongst themselves. It is hoped that some light may be shed on the causes of these differential mortalities in a subsequent publication in which the hydrography and macro-plankton of the area will be discussed.

From the present data the best index of the recruitment to the adult stock ought to be the adundance of larvae in June. These, however, cover a considerable and variable size range between years for which some compensation must be made. For this purpose the size range has been divided into those up to 18 mm and those over 18 mm. If one takes the means of these size ranges and assumes a mortality of 5% per day between these stages, then those in the larger group have to be increased two and a half times to give the equivalent of those in the smaller group. If the larvae are then reduced to the mean number under 10 sq. metres of surface one gets for the indices of abundance, 1950—1·2, 1952—2·35 and 1953—2·67. As there was no June cruise in 1951 no such index is available for that year. No complete measure has yet been made of the contribution to the fishable stock by these broods. The estimates of the abundance of these broods in their first year of life by Jones (1951), and Jones and Main (1952-54) is, 1950—228, 1952—488 and 1953—490—which shows a very satisfactory degree of agreement.

Another but less reliable, approach, which gives a figure for 1951 also, is to apply the mortality coefficients given above to the relative egg spawning assessments, so as to calculate the number of larvae attaining a size of 25 mm in each year. On this basis one gets the following figures:——1950—398×10^7, 1951—1930×10^7, 1952—517×10^7, 1953—493×10^7. These again show some agreement with Jones' and Main's figures of 228, 538, 488 and 495 respectively for numbers of O-group, in the research trawl catches, except that the figure for survival to 25 mm in 1951 is distinctly higher in proportion to the other years than is the corresponding trawl catch. A possible explanation may be that, as there was no June cruise in 1951, it had to be assumed that the mortality rate found in May would apply in June also, whereas it may well have been too low! On the whole, however, for 1950, 1952 and 1953, there is a satisfactory degree of agreement, which would suggest that over these years at least no significant differential mortality occurred beyond a size of 25 mm.

DISCUSSION

As was stated in the Introduction, the impetus to this investigation was provided by Parrish's (1950) findings for North Sea haddock, that the abundance of a year brood is independent of the size of the stock which spawned it, and that the contribution of a brood to the fishable stock is already determined in its first year of life. It appeared reasonable, therefore, to try to extend these findings by an investigation of the planktonic stages of the species. The essential data on pp 16-24 are drawn together in Table IX for convenience. It is unfortunate that, over the period concerned, annual variations from breeding stocks to brood were relatively small. Within those limits it seems reasonable to draw certain conclusions.

TABLE IX

	1950	1951	1952	1953
Size of Spawning Stock (weighted catch per 100 hrs. see p. 19)	164	176	140	110
Total Annual Egg Production (see pp. 16–20)	58×10^{11}	70×10^{11}	67×10^{11}	49×10^{11}
Index of Larval Abundance in June (see p. 24)	280×10^{7}	—	548×10^{7}	622×10^{7}
Abundance of Brood in First Year of Life (Numbers per 10 hrs. fishing, see p. 24) ..	228	538	488	490

The first step seemed to be to relate the actual egg production to the spawning potential of the stock. It is conceivable that egg production might vary between seasons independently of variation in the mature population, because of differences in the proportions of the adult stock producing mature eggs, of differential fecundities between years, or of differences in the efficiency of fertilisation. The data presented suggest that over these four years the annual egg production was reasonably related to the size of the adult stock producing it, so that within the level of variation encountered the success of the brood was independent of the initial egg production as well as of the spawning stock.

Parrish also found evidence that the size of a year brood is already determined before it takes to demersal life. The present investigation has shown that the abundance of pelagic larvae in June provides a reliable index of the abundance of the brood in its first year of benthic life. This, taken in conjunction with Parrish's conclusion, implies that the differential mortality which contributes towards brood fluctuations must occur in the planktonic stage before a size of 25 mm is obtained. This is shown in the present material by the differential planktonic mortality between the 1950 and the other broods of larvae. Within the range of variation experienced in these years the level of recruitment was independent of the number of eggs spawned.

It is particularly unfortunate that none of these four years yielded either a conspicuously successful or a peculiarly poor brood year, and we are left with only the moderately poor year of 1950 from which to draw conclusions regarding the factors operating in brood survival. Three points seem significant in regard to the history of this year. Firstly, the number of eggs spawned during the season was at least up to the average for the other years and higher than that of 1953. Secondly, the eggs spawned in March had an above-average survival rate throughout their planktonic phase but were too few initially to affect significantly the success of the brood. Thirdly, the failure of the eggs spawned at the peak of the season appeared to be due rather to a continuously higher than average mortality throughout their planktonic phase than to a short period of cataclysmic mortality.

SUMMARY

1. The Faroe area was continuously sampled in a series of cruises during the planktonic phase of the haddock in each of the years 1950–1953.

2. A method is described of estimating the number of cod and haddock eggs in mixed populations of the two species. The spawning season and spawning areas of the haddock at Faroe are more accurately delineated than has been done previously and the distribution of the larvae discussed.

3. The growth rate of haddock larvae is discussed—the data are best fitted by assuming exponential growth with an increase of 0·012 per day in the logarithms of the length. The annual egg production for each of the four seasons has been estimated and related to the size of the spawning stock.

4. The abundance of larvae and their rates of mortality are discussed and related to brood recruitment. The below-average recruitment of the 1950 brood would seem to have been caused by a higher than normal mortality operating throughout the entire planktonic phase on the eggs spawned at the peak of the spawning season. Within the range of variation experienced in these years the level of recruitment was independent of the number of eggs spawned.

REFERENCES

Ahlstrom, E. H. 1948. 'A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941.' Spec. sci. Rep. U.S. Fish Wildl. Serv., No. 54.

Anon. 1952. Progr. Rep. Calif. Sardine Res., 1 Jan. 1951–30 June 1952.

Apstein, C. 1909. 'Die Bestimmung des Alters pelagisch lebender Fischeier.' Mitt. dtsch. SeefischVer., **25**, 364.

Cushing, D. H. 1953. 'Studies on plankton populations.' J. Cons. int. Explor. Mer, **19**, 3.

Dannevig, H. 1895. 'The influence of temperature on the development of the eggs of fishes.' Rep. Fish. Bd. Scot., **13** (3), 147.

Fisher, R. A. 1954. 'Statistical Methods for Research Workers,' 12th ed., pp. XV + 356. Edinburgh: Oliver & Boyd.

Harding, J. P. 1949. 'The use of probability paper for the graphical analysis of polymodal frequency distributions.' J. Mar. biol. Ass. U.K., **28**, 141.

Heincke, F. and Ehrenbaum, E. 1900. 'Eier und Larven von Fischen der deutschen Bucht.' Wiss. Meeresuntersuch., Abt. Helgoland, **3**, 131.

Hjort, J. 1926. 'Fluctuations in the year classes of important food fishes.' J. Cons. int. Explor. Mer, **1**, 5.

Jones, R. 1951. Ann. biol., Copenhague, **7**, 28.

Jones, R. and Main, W. 1952. Ann. biol., Copenhague, **8**, 36.

—— —— 1953. Ann. biol., Copenhague, **9**, 35.

—— —— 1954. Ann. biol., Copenhague, **10**, 32.

Marshall, N. B. 1948. 'Continuous plankton records: zooplankton (other than Copepoda and young fish) in the North Sea, 1938–1939.' Hull Bull. Mar. Ecol., **2** (13), 173.

Parrish, B. B. 1950. 'Brood fluctuations in the North Sea haddock population.' Challenger Soc. Abstracts, **3** (2) 18.

Rae, K. M. and Fraser, J. H. 1941. 'Ecological investigations with the continuous plankton recorder: the Copepoda of the southern North Sea, 1932–37.' Hull Bull. Mar. Ecol., **1** (4), 171.

Raitt, D. S. 1933. 'The fecundity of the haddock.' Sci. Invest. Fish. Scot., 1932, No. 1.

Russell, F. S. 1926. 'The vertical distribution of marine macroplankton. 3. Diurnal observations on the pelagic young of teleostean fishes in the Plymouth area.' J. Mar. biol. Ass. U.K., **14**, 387.

Schmidt, J. 1909. 'The distribution of the pelagic fry and the spawning regions of the gadoids in the North Atlantic from Iceland to Spain.' Rapp. Cons. Explor. Mer, **10**, B.4.

Sette, O. E. 1943. 'Biology of the Atlantic mackerel (*Scomber scombrus*) of North America, Pt. 1: early life history.' Fish. Bull., U.S., **50**, 149.

SETTE, O. E. and AHLSTROM, E. H. 1948. 'Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941.' J. Mar. Res., **7**, 511.

SHEARD, K. 1941. 'Improved methods of collecting marine organisms.' Rec. S. Aust. Mus., **7**, 11.

TAIT, J. B. 1934. 'Surface drift-bottle results in relation to temperature, salinity and density distributions in the northern North Sea.' Rapp. Cons. Explor. Mer, **89** (3), 69.

WALFORD, L. A. 1938. 'Effect of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank.' Bull. U.S. Bur. Fish., **49**, 1.

WINSOR, C. P. and CLARKE, G. L. 1940. 'A statistical study of variation in the catch of plankton nets.' J. Mar. Res., **3**, 1.

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